# Historical Zoogeographic Study of the Clavagellacea

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(2 Textfigures)

## *Introduction*

The restudy of this unusual pelecypod group, often referred to as the "watering pot" shells, was undertaken as a revision for the "Treatise on Invertebrate Paleontology" in which a resumé of the taxa and types of the superfamily will appear. A more complete review of the group was published in The Veliger, volume 4, number 4 (Smith, 1962).

During the investigation it was necessary to compile data on the relationships of over 100 species of the group. Interesting and somewhat puzzling distribution patterns emerged for species and higher taxa in both time and space. I am, therefore, attempting an analysis of the distribution patterns in the light of modern zoogeographic thought.

Apparent rarity of the clavagellids during all of their geologic history makes it difficult to arrive at other than hypothetical conclusions. There are no large numbers of fossil remains nor of living forms upon which to base statistical analyses. Sparsity of the animals at any one time, and perhaps also difficulty of preservation in their usual habitats, have left pitifully incomplete the record of their geologic history. One is further hampered by incomplete studies of geologic sections in areas of clavagellid distribution outside Europe.

The present study should at least point up the necessity of taking into consideration the geologic record in zoogeographic investigations, regardless of the incompleteness of that record. In the case of clavagellids, restriction to data on the Recent species would give the reverse of what is probably the true history of the group. There are only four species living outside the Indo-Pacific-Australasian region, yet most of the group's geologic history is recorded in the strata of Europe. Indeed, it would be difficult to explain the present distribution without some knowledge of past occurrences.

Historical zoogeography is neither clearly a means nor an end. It must depend upon almost every other discipline of the geologic and biologic sciences. The historical zoogeographer is accountable for the consideration of an ever-increasing bulk of data, from paleontology to pollution studies. At the present time he is torn between revelling in the tremendous volume of available data and being crushed by its mass. After consideration of the already formidable amount of data, he attempts to integrate his own and thus adds to the task of those who follow.

The extreme importance of both temperatures and land-mass distribution in the control of shelf faunas requires the careful consideration of paleoclimates and paleogeography, each of which is a synthesis of data from multiple-discipline approaches. Historical zoogeography must both use and test the earlier findings of diverse and often seemingly alien workers.

## *Relationships and Distribution*

The two figures following will summarize as briefly as possible the findings of the earlier study (Smith, loc. cit.). Figure 1 diagrammatically represents the development of the clavagellids throughout their known geologic history. Morphology and geographic distributions suggest that the penicillids arose in Early Tertiary from Clavagella (Stirpulina) and that the rock-dwelling forms are later developments from Clavagella s. s.

Figure 2 shows the change in geographic distribution of the group's members with advancing time. The eastward shift during later Tertiary times is evident. The available geologic record indicates that the group inhabited mainly European waters until Late Oligocene. Bryopa is the only known survivor west of the Red Sea.

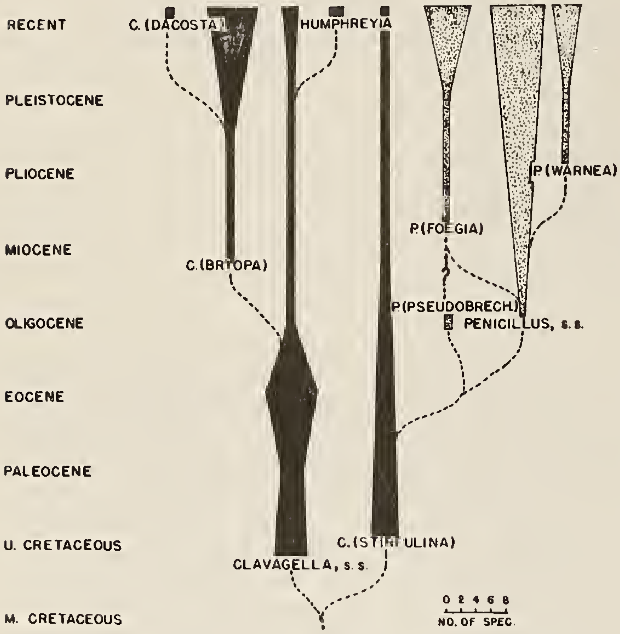


Figure 1. Temporal distribution of Clavagellids and probable evolutionary development

Modern clavagellids inhabit mainly clear shallow seas in subtropical shelf areas. The center of present-day clavagellid distribution lies in the vast areas of submerged shelf surrounding the Indo-Malay archipelago, from southern Japan to the northern shores of Australia, and as far west as the Mediterranean.

It is important to note that, as members of the subtropical shelf faunas, the clavagellids must have required temperature and land area distributions differing from those of the modern world to allow (or force) their eastward movements during Middle to Late Tertiary times. Affinities have been noted in many animal groups between inhabitants of southwestern Mediterranean and subtropical Japanese waters. Numerous fossil occurrences of their relatives in present-day land areas such as India also attest to the presence of a former connecting seaway. This ancient water body — the Tethys Sea — extended, approximately through the modern Mediterranean area, from eastern North America to southern Asia, and existed from Early Mesozoic to Middle Tertiary times.

## *Historical Zoogeography of the Clavagellids*

During Late Cretaceous time continental terrestrial areas were considerably restricted, and the areal extent of epicontinental seas was greater than at any time since Ordovician (Zeuner, 1945). The continents were comparatively featureless, rather uniformly low in elevation. Tropical to subtropical floras occupied most of the southern two-thirds of the United States (MacGinitie, 1958). According to Durham (1950), the February isotherm of 18° C. must have been located at about 53° N. Lat., approximately 1'500 miles north of its present location on the coast of Baja California. Suggested warmth of the seas would be sufficient to push subtropical faunas to the northern limits of the Tethys seaway.

The Tethys existed for much of geologic history; but, being considerably north of the equator, it perhaps provided east-west passage of tropical, and to some extent subtropical, marine faunas only during warmest times, e. g., Late Cretaceous to Late Eocene. According to Schuchert (1935), there existed shallow shelf areas bordering continuous lands which connected the European (about present-day Spain) with the North American region (about New York). During the warm Late Cretaceous, this could have provided the westward migration passage for subtropical shelf faunas necessary for the appearance of Clavagella (Stirpulina) armata Morton in the Late Cretaceous of New Jersey. Continued warming then perhaps forced them back to the northeast along the coast beyond the limits of the present North American continent, and thus outside the areas of our present exposures of younger strata. Similarly, the Tethys seaway provided even easier access for subtropical shelf faunas to the northern Indian area during Late Cretaceous, as the connection of India with the Mediterranean region

| | NORTH AMERICA | EUROPE | AFRICA | RED SEA | INDIA | INDO-PACIFIC | JAPAN-PHILIP. | AUSTRALASIA |
|---|---|---|---|---|---|---|---|---|
| RECENT | | C.(B.) | | P.(Pe.)<br>P.(W.) | | C.(B.)<br>P.(Pe.)<br>P.(F.) | C.(C.)<br>C.(S.)<br>P.(Pe.)<br>P.(F.)<br>P.(W.) | C.(C.)<br>C.(B.)<br>C.(D.)<br>H.<br>P.(Pe.)<br>P.(F.)<br>P.(W.) |
| PLEISTOCENE | | | | | | P.(Pe.) | | |
| PLIOCENE | | C.(C.)<br>C.(S.) | | P.(Pe.) | | P.(Pe.)<br>P.(F.) | P.(F.)<br>P.(W.) | |
| MIOCENE | | C.(S.) | | | C (C) | P.(Pe.)<br>P.(F.) | P.(F.) | |
| OLIGOCENE | | P.(Ps.)<br>C.(B.)<br>C (C)<br>C.(S.) | | C (S) | | P.(Pe.) | | |
| EOCENE | | C (C) | | | | | | |
| PALEOCENE | | C.(S.)<br>C.(C.) | | | | | | |
| U. CRETACEOUS | C (S) | C.(S)<br>C.(C.) | C (C) | | C (C) | | | |

Figure 2. Geographic distribution of Clavagellids from Late Cretaceous to Recent

is well established. This should adequately explain the presence of Clavagella (Clavagella) semisulcata Forbes in Late Cretaceous strata of India.

Questionable Middle Cretaceous occurrences of Clavagella s. s. and its morphology suggest that it is the original stock and perhaps developed in the shelf areas of warm shallow seas of southern Europe. The lack of records from the southern hemisphere suggests that it was not a tropical form but originated in the northern subtropics prior to the Late Cretaceous-Early Tertiary temperature maximum.

Continued warming and access to the entire Tethys seaway suggest the possible avenue for eastward migration of Clavagella s. s. (to India) and westward migration to North America of the then new C. (Stirpulina) branch. As the only living Stirpulina is found in Japanese waters, it may be inferred that it was tolerant of slightly colder waters and was thus able to negotiate the more northerly route to North America, whereas Clavagella s. s. could not. The suggestion that Stirpulina was the colder water form of the two is strengthened by the fact that in the cooler Pliocene the animal was still living in Central Europe, whereas Clavagella s. s. is not found in Pliocene strata outside the Italian peninsula.

## *Paleocene - Eocene*

"Existent bitter arctic conditions around the poles would not be possible with the indicated oceanic temperatures of Late Cretaceous and Early Tertiary times" (MacGinitie, 1958). Chaney (1947) reported evidence which indicates the existence of temperate deciduous forests around the North Pole ranging in age from Paleocene to Middle Eocene. Durham (1950) concluded that during the Eocene, the 18° C. isotherm was between 53° and 55° North Latitude, even farther north than during Late Cretaceous. Tropical floras existed along the Gulf of Mexico during Early Tertiary and shifted northward, the advance culminating in Late Eocene (Chaney, 1947).

After spreading as far as India and eastern North America during Late Cretaceous, no Paleocene or Eocene records of clavagellids are known from areas outside Europe. This suggests that, for some reason, east-west migration was halted by the end of Cretaceous and the group was forced to withdraw to the European region. The configuration of the northern shores of the Tethys seaway may be offered as a reason for the apparent withdrawal to the central area. Since the clavagellids were apparently members of the subtropical shelf faunas, the continued rise in temperatures through Eocene would force northward migration (northwest from India and northeast from North America) along the northern arc of the Tethys Sea. This hypothesis is negatively supported by the lack of Eocene occurrences in southern Europe. It would be positively supported by the discovery of Eocene clavagellids in Greenland and on the Scandinavian peninsula.

## *Oligocene*

Emiliani (1958), from his study of deep sea cores, has indicated that in the Pacific abyssal equatorial temperatures of Middle Oligocene were about 10° C., and present-day circulation patterns suggest that temperatures must have been little less in the polar seas. Although polar winter snows would be probable, permanent ice caps would be impossible under such conditions. The time from Early Oligocene to the first glacial stage of Pleistocene is marked by a gradual cooling and drying of climates (MacGinitie, 1958).

The decline of temperatures in Oligocene again allowed south and southeastward migration of the subtropical shelf faunas. Perhaps discontinuous land and shelf areas existed between Europe and North America, effectively restricting a remigration to the west. Clavagellids returned to southern Europe and northeastern Africa, and three new branches developed to take advantage of the available environments.

Penicillus s. l. probably developed in the northern Tethys, perhaps during Early Oligocene. Continued lowering of temperatures would have brought it south into Europe (Pseudobrechites) and southeastward along the unbroken northeastern shore of the Tethys Sea into the Indo-Pacific region (Penicillus s. s.). The form Bryopa developed in the southern European area in Late Oligocene, perhaps replacing some tropical form which was probably forced to abandon its niche among the declining reef corals as the lowering of temperatures continued. The continued increase of climatic extremes apparently eliminated Pseudobrechites in the south-central Tethys and left Penicillus alone in the Indo-Pacific area, from which all later penicillids must have branched.

## *Neogene and Quaternary in Europe*

According to Durham (1950), the 18° C. isotherm had moved down the west coast of America to the approximate latitude of northern California by Early Miocene. This indicates the continued lowering of general oceanic temperatures which eventually brought about the decline of the tropical and subtropical Tethys faunas in the European area. This is evidenced by the restriction of many groups such as the reef corals, and their migration into the Indo-Pacific region (Gerth, 1925, in Ekman, 1953).

During Miocene times Clavagella s. s. appeared in the Indian region, probably moving southeastward with other subtropical elements of the Tethys fauna. During Pliocene only Stirpulina remained in the central European area, and Clavagella s. s. was effectively restricted to the southern extremities of that continent.

Bryopa, which developed during cooler times than other clavagellids, was the only form to survive Pleistocene coldness in the Mediterranean region. It is possible that, since Bryopa migrated with other faunas into the Indo-Pacific region before effective closing of the Tethys seaway, it may have been reintroduced into the Mediterranean through the Red Sea during an interglacial stage of Pleistocene. There is, however, no supporting evidence from Pleistocene strata for such a supposition.

## *Early Neogene in the Indo-West-Pacific*

The Oligocene introduction of Penicillus s. s. into the Indo-Pacific region opened new vistas for the development of the penicillid branch. Clavagella s. s., Bryopa, and Stirpulina survived the migration also but were probably equatorially restricted much earlier than the newer forms. Penicillus, which developed during cooler Middle Tertiary time, was apparently able to make the most of vast shelf areas of the Indo-Malay region for rapid spread and the development of several new branches.

During Miocene the penicillid Foegia developed in the Indo-Malay area and migrated northeastward into the southern Japanese and Philippines region. Clavagella remained along the shores of the Indian Ocean and Penicillus s. s. developed new species and spread through the Indo-Pacific.

## *Pliocene*

Axelrod (1956, 1957) has suggested from paleobotanical evidence that average temperatures at the beginning of Pliocene differed little from those of today but suggested that the temperature range was considerably less in the western United States (more equable climates). However, the northern oceans were apparently still warmer than those of today, as Durham (1950) suggests a position for the 18° C. isotherm at 35° N. Latitude, some 5° to 6° north of its present location. From distribution studies of fossil pulmonates, Frye & Leonard (1957) concluded that conditions of seasonal climates essentially like the present day were attained by Late Pliocene.

A third penicillid group (Warnea) appeared in the South China Sea and is recorded from Pliocene strata of both Formosa and southern Japan. The Red Sea, much as we know it today — though a little cooler — came into existence during Pliocene, and equable climates allowed considerable spreading of the more eurythermal forms.

Penicillus s. s. migrated into the Red Sea from the Indian Ocean. The higher than normal temperatures of that body of water were perhaps extant even then and may have made it possible for Penicillus to remain there until the present day.

## *Pleistocene*

During the glacial stages the zone of maximum cyclonic activity was even farther south than at present. Southward movement of the polar front and increased temperature gradients caused pluvial conditions in the zone just south of the glaciated area during glacial periods (MacGinitie, 1958). Manley (1955) indicated that north-south temperature gradients may have had at least double the present value. During such times of cyclic climatic changes, the stimuli to admixture, hybridization, and natural selection must have been greatly intensified (MacGinitie, 1958).

During periods of intense glaciation, all clavagellids except Stirpulina were probably restricted to a narrow equatorial zone, being allowed northward and southward migration only during interglacial warming. Only such a distribution would effectively explain the present-day bipolarity of all except Stirpulina and branches developed during Recent times.

## *Recent*

A gradual warming of world climates culminated in the so-called "Climatic-Optimum" about 6 000 years ago, followed by a return to the cooler conditions of the present day. Now, warming seems to have been renewed (MacGinitie, 1958), resulting in the spread of tropical deserts from western India across the Mediterranean and northern Africa, and in the southwestern United States (Wadia, 1955).

The Recent so-called "Climatic Optimum" (actually a post-Pleistocene interglacial stage) probably brought about bipolarity in most of the formerly equatorial groups. Gradual cooling has since allowed equatorial mingling of the essentially tropical forms.

Two new groups, Humphreyia and Dacosta, have developed on the Australian coasts, probably from the clavagellid line. Warnea probably migrated around the shores of the Indian Ocean and into the Red Sea during an interglacial stage, or perhaps during the Early Recent warming. Subsequent cooling has eliminated it from intermediate areas, but adjacent desert conditions have maintained higher than normal temperatures in the Red Sea and Warnea has survived there.

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